Journal of Research on the Lepidoptera 20(1): 18-35, 1981(82)

Geographic Variation and Ecology of *Hesperia leonardus* (Hesperiidae)

James A. Scott

and

Ray E. Stanford

60 Estes Street, Lakewood, Colorado 80226 and
720 Fairfax Street, Denver, Colorado 80220

Abstract. The systematics of the eastern members of the *Hesperia leonardus* complex are studied. *H. l. leonardus* and *H. l. pawnee* are conspecific and intergrade in Minnesota, Wisconsin and elsewhere, where extremely variable populations exist. The name *H. l. montana* is restricted to a recently rediscovered third subspecies occupying a small area in the Colorado mountains. *H. l. montana* is also extremely variable and is similar in several characteristics to Minnesota intergrade specimens. We summarize what is known about distribution, flight periods, habitat, adult behavior and foodplants of the *leonardus* complex. Adults have one brood (mostly August-September), and western populations feed mainly on *Liatris* flowers. Larvae eat various grasses, and hibernate in the first stage.

Introduction

MacNeill (1964) defined the *H. leonardus* group to include two western species (*columbia* Scudder and *pahaska* Leussler) which he studied in detail, and two eastern entities not studied in detail, *pawnee* and *leonardus*. The purpose of this paper is to study the taxonomic relationships of the latter two entities and to summarize what is known of their variation, distribution, behavior and early stages. The most interesting feature of the complex is that the eastern members *pawnee* and *leonardus*, appear to belong to one species, despite the gross color difference between them. Because of the importance of this conspecificity, the evidence for it is presented first.

Conspecificity of *leonardus* and *pawnee*

There are several reasons why we combine *leonardus* and *pawnee* into one species. Pupae are the same (Scott, 1975b; Dethier, 1948). Larvae are the same although *H. l. pawnee* heads are lighter than those of *H. l. leonardus* and *H. l. montana* (Scott, 1975b). Scudder's (1889) drawings of first instar *leonardus* leave out many setae which occur in all known *Hesperia* species, and the long lateral setae on the ninth abdominal

segment in his drawing is probably a short spatulate seta as in all other known *Hesperia* (Dethier, 1939; Scott, 1975b). Eggs are very similar (Scott, 1975b) (the egg figured by Scudder (1889) is again poorly drawn). There are no differences in male or female genitalia which we can detect. Genitalia are too variable individually to detect differences; the genitalia drawings of *pawnee* and *leonardus* by MacNeill (1964) are not "typical". There may be slight interpopulational differences in antennal shaft length, the number of segments of the antennal shaft, and the length of the male penultimate tarsal segment, but these characteristics are also variable. Flight periods and adult behavior are very similar.

The main differences between populations of *leonardus* involve color pattern of palpi, body and wings. Superficially populations and individuals look very different from one another (Figs. 2-5).

H. l. leonardus and *H. l. pawnee* apparently intergrade over a broad area from Minnesota and Wisconsin to Manitoba and perhaps Iowa (Fig. 1). In Spruce Woods Forest in southern Manitoba individuals resemble *pawnee* but often have a rust tinge to the ventral yellow color, especially in females (Figs. 2-3). Four males from Sandilands in southeastern Manitoba are like Ontario *H. l. leonardus* except the dorsal surface is a little lighter, and the ventral hindwing spots are small. Samples of *H. l. leonardus* from Crivitz, Wisconsin are odd in several respects and several characters tend in the direction of *pawnee* (Figs. 2-3). Northwestern Wisconsin samples are intermediate to *H. l. pawnee* and *H. l. leonardus*. Of the two males from Des Moines, Iowa (Carnegie Museum), "one of these is quite like eastern *leonardus*, the other is somewhat paler, more fulvous, suggests transition to *pawnee*, but still mostly like *leonardus*" (H. K. Clench, pers. comm.).

The central Minnesota population is extremely variable in every wing character, varying from nearly "typical" *pawnee* to nearly "typical" *leonardus* in every character. The few structural characters such as antennal shaft length to head width ratio are also variable and are intermediate between the two subspecies.

If there are no barriers to hybridization of *H. l. leonardus* and *H. l. pawnee*, mating should be random and after several generations non-linked genes should be independently combined in offspring. If major barriers to hybridization occur, however, or hybrids are largely sterile, the population should consist of a majority of individuals recognizable as either *H. l. leonardus* or *H. l. pawnee* plus a minority of individuals with hybrid traits. The evidence strongly suggests the first interpretation for the central Minnesota population.

In an effort to analyze differences between *H. l. leonardus* and *H. l. pawnee*, four male characters and five female characters were chosen for quantitative analysis. These characters were: (1) Ventral hindwing color (rated from 0 to 7 using eight standard reference specimens varying from light yellow to deep red brown). This color varies from yellow as in *H. l.*

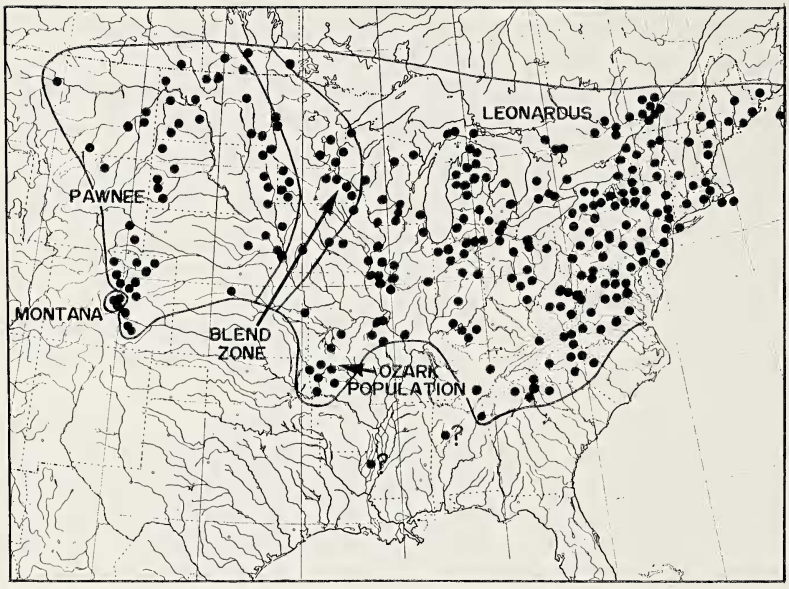
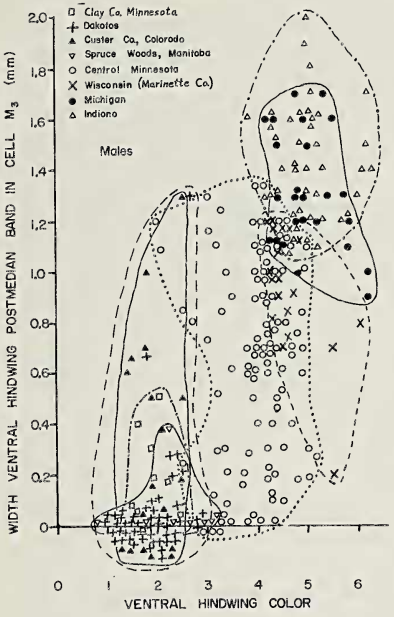
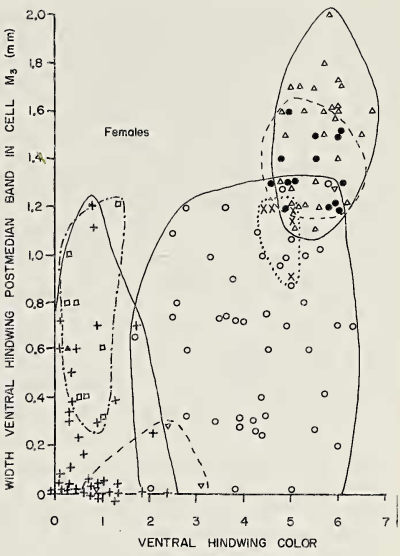


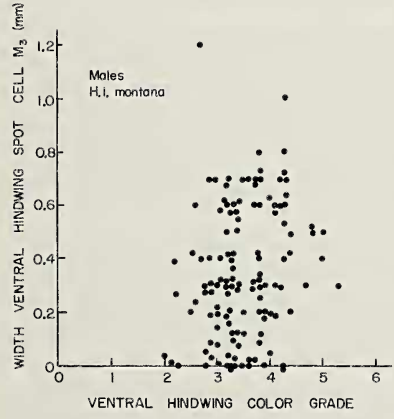
Fig. 1. Map of *H. leonardus* populations.

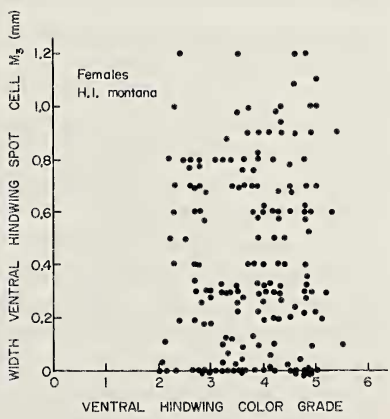
pawnee to red brown as in *H. l. leonardus* in both sexes (Figs. 2-3). (2) The width of the ventral hindwing postmedian band in cell M^3. This band varies from 0 as in *H. l. pawnee* to 1.4 mm as in *H. l. leonardus* in both sexes (Figs. 2-3). (3) Dorsal lightness varies from dark reddish as in *H. l. leonardus* to light fulvous as in *H. l. pawnee* in both sexes. This character was quantified by use of five reference specimens. (4) Darkness of ventral forewing tornus. This varies from the ground color as in *H. l. pawnee* to completely black as in *H. l. leonardus* in both sexes. Five reference specimens were also used. (5) Transparency of the dorsal forewing hyaline spot. This character was used for females only. This spot varies from the ground color as in *H. l. leonardus*, to transparent as in *H. l. pawnee*. Four reference specimens were used to quantify this character. Characters 1-5 are very variable in the *leonardus* X *pawnee* blend zone, much more than in either *H. l. leonardus* or *H. l. pawnee*.

Characters 1-5 were plotted against each other (two of the 14 plots are shown, Figs. 2-5) in an effort to discover whether there was any reproductive isolation between *leonardus* and *pawnee* that would show up in wing pattern. No correlations were found except that there are very slight correlations in both sexes between dorsal lightness and darkness of the ventral forewing tornus, and in females (but not males) slight correlations appeared between ventral hindwing color and dorsal lightness and between ventral hindwing color and darkness of ventral forewing









Figs. 2-5. Scatter diagrams of width of ventral hindwing postmedian spot in cell M^3 versus ventral hindwing color (0-pale yellow, to 6-dark rust red (for ssp. *leonardus*) or 6-dark brown (for ssp. *montana*)). Most ssp. are on Figs. 2-3, but ssp. *montana* is on Figs. 4-5.

tornus. These correlations were very small however, and merely indicate that in some cases, especially in females, if one part of the wing is light another part is slightly likely to be light as well.

In general, however, these five characters which distinguish *H. l. leonardus* from *H. l. pawnee* are not correlated with each other. A typical Minnesota individual may have one character tending toward *H. l. leonardus*, another tendig toward *H. l. pawnee*, and others intermediate. It is our opinion that recombinations have occurred resulting in individuals with characteristics not observed in *H. l. pawnee* and *H. l. leonardus* populations. For example, some individuals have the ventral hindwing rust-red but with very small or no spots, and other individuals have this area light yellow with large spots (Figs. 2-3). This lack of correlation of characters and the lack of two clusters of individuals corresponding to the two parental types in any character suggests that the central Minnesota population is a freely interbreeding population. Due to fragmentation of natural habitat by farmland the central Minnesota colonies probably now receive little gene flow from either *H. l. leonardus* or *H. l. pawnee*, and variability is maintained as in *H. l. montana* through unknown mechanisms.

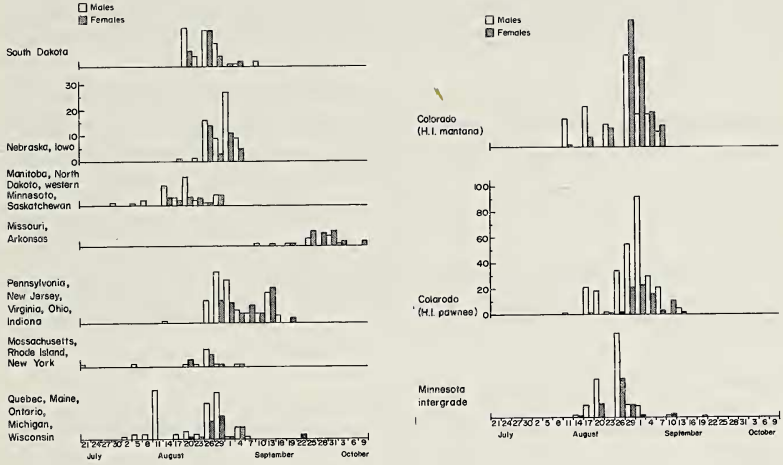
Males from Wabasha County, Minnesota in this intergradation area show variation similar to that of specimens from Anoka and Sherburne counties. Females, however, are slightly more similar to *H. l. leonardus* than are females from the latter two counties. Of 10 females examined, five are in the *leonardus* part of the Minnesota population scattergram (Fig. 3), while the other five are scattered but not in the *pawnee* corner of the plot.

Flight Period, Habitat, Behavior and Larval Biology

The flight period of *H. leonardus* is very similar throughout the range: one brood, usually August to September (Figs. 6-7). Figures 6-7 clearly show that flight period is earlier at higher latitude and higher altitude. Ozark populations fly six weeks later than Canada populations, and plains *H. l. pawnee* flies later than mountain *H. l. montana*. Pittsburgh, Pennsylvania, inland populations fly several weeks earlier than those on the coast at Philadelphia.

H. leonardus populations all occur in meadows or grasslands, commonly old fields and moist meadows for *H. l. leonardus*, sandy prairie (near wooded areas) for the central Minnesota intergrade populations, prairie (sometimes sandy) for *H. l. pawnee*, and open grassy pine forest for *H. l. montana*.

Adult behavior of *leonardus* populations is very similar. All three subspecies and the intergrade populations are common at *Liatris punctata* flowers in Colorado, Nebraska, Minnesota, Michigan and New Jersey (occasionally on other flowers such as *Cirsium, Vernonia angustifolia, Eupatorium purpureum, Solidago, Clematis, Aster,* other *Liatris* species, "bonehead"). *H. l. leonardus* is usually found on flowers other than *Liatris*,



Figs. 6-7. Flight period for males and females, in three-day intervals.

commonly on high flowers. Adults are not often seen away from flowers. *H. l. leonardus* males commonly choose high perches (4-5 ft.), whereas western populations usually choose lower perches. *H. l. pawnee* males when not feeding often perch on small to large hilltops throughout the day. *H. l. montana* males are usually found in concentrations with females, often on small hills; males have not been found away from these concentrations on nearby hilltops used earlier in the summer by *H. pahaska* males. Unsuccessful courtship of unwilling females appears identical in *H. l. montana, H. l. pawnee* and *H. l. leonardus*. It occurs throughout the day, often on flowers, as males attempt to mate with feeding females, who flutter their wings until courtship terminates.

H. l. leonardus foodplants are *Agrostis* (Scudder, 1893), *Panicum virgatum* and *Eragrostis alba* (Shapiro, 1966). Tietz (1972) lists a dicotyledon which cannot be a foodplant. Dethier (1939) and Scudder (1889) raised *H. l. leonardus* in the laboratory on common grasses. Many ovipositions of *H. l. montana* were seen on *Bouteloua gracilis*. We have not discovered oviposition substrate or foodplant for *H. l. pawnee*. A record of larval host of *pawnee* (1970 season's summary of the Lepidopterists' Society and Ferris, 1971) is erroneous because it is based on laboratory feeding of a dying larva. We raised *H. l. montana* and *H. l. pawnee* to adults (Scott, 1975b) on *Poa pratensis, Cynodon dactylon* and other unidentified

grasses, and believe that laboratory hosts have little relevance to the plant used in nature by Hesperiinae, which may be host-specific in nature in spite of broad larval tolerance for laboratory grasses. Some *Hesperia* oviposit rather haphazardly, however (Scott, 1975a), so larvae may not be host-specific.

All *H. leonardus* populations must overwinter as young larvae, because eggs hatch immediately and there is not enough time before winter for the larvae to grow to large size. Overwintering occurs as first stage larva (ssp. *montana*), young larva (Scudder, 1893), first stage larva (Scudder, 1889), most first and some second stage larva (Dethier, 1939), second instar (Laurent, 1908) (all ssp. *leonardus*). When *H. l. leonardus, H. l. pawnee* and *H. l. montana* are raised indoors, no diapause occurs and adults emerge from November to January, taking only about three months to develop (Scott, 1975b).

Taxonomy—*H. l. leonardus*

leonardus Harris, 1862. Ins. Inj. Veget., p. 314. Type locality: Boston, Mass.

lidia Plotz, 1883 (nomen dubium, dos Passos, 1964).

liberia Plotz, 1883 (synonym or nomen dubium; see dos Passos, 1960).

stallingsi H. A. Freeman, 1943. Bull. Brooklyn Ent. Soc. 38: 153. Type locality: Blendon, Franklin Co., Ohio.

This subspecies occurs usually in open fields and damp meadows but occurs in permanently wet meadows and bogs in Virginia (Clark & Clark, 1951).

Description

Apical FW spots distinct, ochre above and below. DFW basal color of females brown with a very slight orange flush. DFW spots of females distinct, fulvous, one or rarely two. VHW color light to dark rust red. VHW spots usually large (very rarely absent), ochre to white (more ochreous in males), median spot in cell Sc + R^1, and median cell spot almost always present and round, spots larger in females. Fulvous DHW spots fairly distinct, moderate fulvous suffusion in males, little in females. VFW tornus almost always black, rarely little lighter than ground color.

Last instar larval head with a light V-shaped genal area and a lateral light area.

Variation within *H. leonardus leonardus* is mostly clinal, with different characters showing different clines or patterns of variation (Table 1). There is essentially a north-south cline in wing size, with a peculiar small sample from Wisconsin. Dark dorsal phenotypes are prevalent on the Ozark Plateau and in the southeast; the most fulvous populations occur in Maine, Pennsylvania, Indiana and Wisconsin. The ventral hindwing band is smallest in the Ozark Plateau. This band is light in the Great Lakes region, and dark (ochraceous) in southern populations. Ventral hindwing color is dark in southern Great Lakes and middle Atlantic regions, lighter (ochreous) northward and westward. The Maine and Ozark samples, greatly different in other characters, are similar in ventral hindwing color. The independent variation of these characters in *l. leonardus* makes designation of additional

subspecies futile.

The Ozark sample is the most distinct. The Ozark material is larger, darker and tends to have the ventral hindwing spots reduced. The synonym *stallingsi* (Freeman, 1943) named from Franklin County, Ohio, falls about in the middle of the range of variation we have observed in *H. l. leonardus.*

H. l. leonardus X H. l. pawnee

In central Minnesota there are extremely variable populations intermediate between the subspecies *leonardus* and *pawnee*. Its variation has already been discussed.

Description

Apical spots distinct, sometimes indistinct and usually ochre ventrally, sometimes white in females. DFW basal color of females moderately ochre to brown. DFW spots of females distinct, most fulvous, some hyaline, usually 1-3, rarely 4 spots. VHW color ochre yellow to light rust red. VHW spots large to obsolete, usually ochreous, median spot cell Sc + R^1 often absent and median cell spot round but often small when macular band is present. Fulvous DHW spots in males sometimes fairly distinct but usually vague due to fulvous suffusion; in females with none to some fulvous suffusion. VFW tornus yellow to black, weakly correlated with ground color, slightly darker in females. Larvae undescribed.

H. l. pawnee (New combination)

Hesperia pawnee Dodge, 1874, Canad. Ent. 6:44. Type locality: Glencoe, Dodge County, Nebraska (type destroyed).

This light colored subspecies has evolved on the Great Plains. Another unrelated species, *Hesperia ottoe* Edwards, has convergently evolved similar appearance with light yellow underside, possibly for camouflage against a background of dried grasses. *H. l. pawnee* differs from *H. l. leonardus* mainly in the much lighter ochre color, the reduction of the ventral spots, and in having hyaline forewing spots in females; *H. l. montana* and the central Minnesota population are variable in the hyaline spot character perhaps due to hydbridization with *pawnee.* The hyaline spots apparently also evolve convergently on the plains. Of the *Hesperia* species which possess hyaline spots, *H. ottoe, H. uncas* Edwards (only plains and eastern Great Basin *uncas* have hyaline spots), *H. dacotae* Skinner, *H. l. pawnee, H. metea* Scudder, *H. attalus* Edwards, and some *H. meskei* Edwards, the first four are plains species.

There is considerable individual variation in some wing characters such as general dorsal color (very light to dark) and the number and size of faint ventral hindwing spots (variation noted also by Leussler, 1923). There is somewhat less variation in ventral color and in color of the female forewing spots. There is very little geographic variation throughout the range. A series from Custer County, Colorado, has slightly larger ventral hindwing ochreous spots (Figs. 2-3). Size decreases clinally from south to north as in *H. l. leonardus* (Table 2). Specimens from Montana are very small.

Table 1.

		Ontario-Quebec	Maine	Massachusetts-Rhode Island	New York	Michigan	Wisconsin	Pennsylvania	New Jersey	Ohio	Indiana	Virginia	Missouri-Arkansas
Sample size	♂	9	15	9	7	28	19	5	22	2	41	4	10
	♀	7	2	7	3	14	5	0	16	3	30	2	23
Forewing length (mm)	♂	14.8	15.1	15.6	15.8	15.2	14.2	15.6	15.4	15.0	15.7	15.9	16.1
	♀	16.1	16.5	16.5	17.0	16.0	15.6	--	16.5	16.2	16.9	17.5	17.1
Dorsal forewing fulvous (1-4)	♂	1.6	2.2	2.2	2.3	1.9	2.0	2.6	1.5	2.0	2.4	1.5	1.7
	♀	2.1	1.5	2.0	2.0	2.2	--	--	2.0	2.0	2.6	2.5	1.7
DHW band suffusion (1-4)	♂	2.2	3.0	2.1	2.3	2.3	2.8	2.6	1.6	2.0	2.6	1.5	1.9
	♀	2.0	1.5	2.0	2.0	2.0	--	--	2.1	2.0	2.3	2.0	1.6
VHW band width (mm)	♂	1.14	1.35	1.33	1.39	1.31	.92	1.28	1.37	1.35	1.43	1.32	1.18
	♀	1.23	1.55	1.43	1.50	1.35	--	--	1.48	1.23	1.48	1.85	.98
VHW band color (1-4)	♂	1.9	2.7	2.7	2.8	2.3	2.6	2.4	2.7	2.0	2.9	3.0	3.0
	♀	2.1	3.0	2.4	3.0	2.4	--	--	2.4	2.7	2.8	3.0	3.0
VHW ground color (0-7)	♂	4.84	4.85	4.44	4.89	5.02	4.67	4.74	5.64	5.65	5.03	5.35	4.29
	♀	5.07	5.45	5.32	5.88	5.43	4.86	--	6.35	5.73	5.59	5.50	5.20

Table 2.

		H. l. leonardus × *H. l. pawnee*	*H. l. pawnee*								*H. l. montana*
		Central Minnesota	W. Minn.	Sask., Man.	Montana	North Dakota	South Dakota	Iowa	Nebraska	Colorado	Colorado
Sample size	♂	104	10	10	7	4	46	5	58	118	126
	♀	45	9	3	0	9	28	1	33	38	175
Forewing length	♂	15.3	16.2	15.0	14.5	15.1	15.5	15.5	15.8	16.0	15.3
	♀	16.6	17.6	17.0	--	16.7	17.3	17.0	17.5	17.4	16.8

Table 1. Geographic variation of six characters for H. leonardus leonardus: (1) forewing length in mm; (2) dorsal forewing fulvous (1-very little fulvous, 4-very fulvous, 2 and 3-intermediate); (3) dorsal hindwing postmedian band suffusion (1-narrow, discrete; 2-broad, still discrete; 3-intermediate; 4-suffused); (4) ventral hindwing postmedian band width in cell M_3 (mm); (5) ventral hindwing postmedian band color (1-white; 2-very light ochre; 3-medium; 4-dark ochre); and (6) ventral hindwing ground color (0-very light yellow; 7-very dark rust red; 1 to 6-intermediate). Numbers (except for sample size) are averages.

Table 2. Forewing length (mm) of *H. leonardus* samples not included in Table 1.

Description

Apical spots rather indistinct and fulvous in males, distinct and hyaline in females. DFW basal color of females moderately ochre to brown. DFW spots of females distinct, most hyaline, usually 3-4, occasionally 2 spots. VHW color of males orangish ochre to ochre yellow, of females light ochre to ochre yellow. VHW spots same as in *montana* but spots usually obsolete, occasionally moderate size and ochreous, little lighter than rest of wing. Fulvous DHW spots same as in *montana*. VFW tornus usually yellow, rarely brown in males and black in females, slightly darker in females.

Larvae as in *leonardus* but heads are lighter laterally.

H. l. montana (New combination)

Pamphila pawnee montana Skinner, 1911, Ent. News 22: 413. Type locality: we restrict to Buffalo Creek, Jefferson County, Colorado (the town).

H. l. montana differs from *H. l. pawnee* mainly in darker (more brown) color and the presence of ventral hindwing spots (Figs. 2-5). It is almost as variable as the Minnesota intergrade population.

Description

Apical spots usually distinct, mostly fulvous, often hyaline in females. DFW basal color of females moderately ochre to brown. DFW spots of females distinct, fulvous to hyaline, most somewhat hyaline, usually 2-3, occasionally 1 or 4 spots. VHW color variable, ochre yellow to dark brown, rarely russet brown or greenish brown. VHW spots moderate size to obsolete, ochreous white, medial spot cell Sc + R^1 rarely present, medial cell spot rounded, often absent, spots larger in females. Fulvous DHW spots fairly distinct, in females with slight to moderately fulvous suffusion, usually lost in fulvous suffusion in males. VFW tornus yellow to black, usually brown, weakly correlated with ground color, slightly darker in females.

Larvae similar to *H. l. leonardus*.

We designate a lectotype male in the Carnegie Museum, Pittsburgh, Pennsylvania (labels include "type no. 7086, Colorado Bruce, Chaffee Co. 7500 ft."), which fits the original description and our characterization of *H. l. montana*. Only two of the eleven cotypes had locality data: one says Chaffee County, Colorado 7500 ft. alt., and the other says Salida (Chaffee County, Colorado), May 21, 7500 ft. alt. These

data are erroneous because *H. leonardus* adults almost never occur before August, the habitat at Salida differs from known habitats, and we have not found the species in Chaffee County in any month despite heavy collecting by James Scott and Glenn Scott (1978). F. M. Brown (pers. comm.) has determined the itinerary of David Bruce, based on letters from Bruce to Herman Strecker. The Chaffee County specimens are obviously mislabeled, because at the time they were collected, Bruce, a painter, was recuperating for three weeks from a fall from a scaffold, in a hospital in Redcloud, Nebraska! F. M. Brown found that Bruce had left a collecting net with the children of Mr. William W. G. Smith at Buffalo Creek, Jefferson County, Colorado, that August, who on 7 September sent Bruce 7 boxes of butterflies from the "Platte Canyon Valley." It seems probable that the Smith children caught the types of *montana* at or near Buffalo Creek. We correct and restrict the type locality to the vicinity of the town of Buffalo Creek, Jefferson County, Colorado, because of these historical records, and because we have found *montana* within several miles of there in August. D. Bruce mislabeled other butterflies (see Ferris & Fisher, 1977), and E. Oslar is similarly noted for mislabeling of material (Oslar specimens in the American Museum of Natural History).

H. l. montana occurs only in a small area in the South Platte River Canyon system in the mountains of Colorado. All the records of *H. l. montana* are in the Pikes Peak Granite, which occurs in the South Platte Canyon southeastward to Pikes Peak. *H. l. pawnee* does not occur on this granite and the granite boundary coincides with the boundary between *montana* and *pawnee*. *H. l. montana* is extremely variable (Figs. 4-5); some specimens are identical to plains *pawnee* and others are brown and have large cream spots on VHW. The ventral hindwing color ranges from yellow to dark brown, usually light brown, with occasional individuals greenish brown or slightly rust brown. In VHW color it is somewhat less variable than the central Minnesota population, but other wing characters are nearly as variable, and show the same lack of correlation as in the central Minnesota population. The variability seems to indicate gene flow from plains *H. l. pawnee*, although we could not find any intervening population between *pawnee* from Waterton and *montana* from the abandoned South Platte Hotel.

The wing pattern differences between *H. l. montana* and *H. l. pawnee* are genetic, because the differences were maintained in individuals raised under identical laboratory conditions.

There are three hypotheses for the origin of *H. l. montana*: 1) introgression of a *pawnee* population with *Hesperia pahaska*; 2) a relict population from a time in the Pleistocene when *H. l. leonardus* occurred in forested areas across what is now the Great Plains and when *H. l. pawnee* was farther south or had not yet evolved; 3) a population which evolved in its present location from *H. l. pawnee* founders. The first hypothesis, introgression, is supported by the several characters in which *H. l. montana* is more similar to *H. pahaska* than to *H. l. pawnee*, and by the flight periods. On the plains the flight periods of *H. pahaska* and *H. l. pawnee* are well separated, but in the mountains *H. l. montana* flies about a week earlier, so that late female *pahaska* might mate with early male *montana*. On July 2 we found *H. pahaska* males hilltopping on hills 200 feet from a later large concentration of *H. l. montana*, but the *H. pahaska* did not differ from specimens found elsewhere in eastern Colorado. In view of the difficulty in proving introgression, hypothesis one must be considered unsupported speculation. In morphology, *H. leonardus* is most

closely related to *H. columbia* which occurs on the pacific Coast. It is less closely related to *H. pahaska*, which is sympatric with *H. l. montana* and *H. l. pawnee* in numerous localities from Colorado to the Dakotas and Montana, but flies in June-July. There is no evidence to suggest that *H. leonardus* and *H. pahaska* hybridize anywhere that they meet, as we previously speculated (MacNeill, 1975). We believe that some combination of hypotheses two and three represents the probable history of the population. Hypothesis two is supported by the lack of dark ventral hindwing phenotypes in the present *H. l. pawnee* population to act as a starting point for selection of a darker population. However, *H. l. leonardus* has rust-red ventral coloration whereas in *l. montana* color variation involves various shades of brown and light rust individuals are rare. If hypothesis two is correct, since *H. l. pawnee* invervened between *l. leonardus* and *l. montana* the latter two populations may have diverged in ventral coloration. Hypothesis three is supported by the fact that both forest subspecies (*leonardus* and *montana*) are dark, whereas the plains subspecies (*pawnee*) is light. The variability of the color pattern of the wings of *H. l. montana* is hard to explain, but could be accounted for by selection for dark spotted phenotypes along with occasional immigration of *H. l. pawnee* phenotypes.

Distribution

Distribution is plotted on Figure 1. Flight periods are shown in Figures 6-7. Localities are listed below. *H. l. leonardus* undoubtedly occurs in Delaware and may be found in eastern Oklahoma. *H. l. leonardus* x *pawnee* may be found in central Iowa, southeastern Nebraska and northeastern Kansas. *H. l. pawnee* may be found in southeastern Alberta. The absence of *H. l. pawnee* records in the center of its range is probably due to lack of collecting.

Several records appear erroneous and are not listed. These include many for *H. l. montana* (see text above); *H. l. leonardus* from Florida (Scudder, 1889) which, judging from the flight period given, refers to *Hesperia attalus* (Edwards); and "Texas" (Evans, 1955). The records for Louisiana and Alabama are so isolated from other records that they require confirmation.

H. leonardus leonardus (counties only for U. S.)
164 males, 107 females examined

Nova Scotia: Digby.

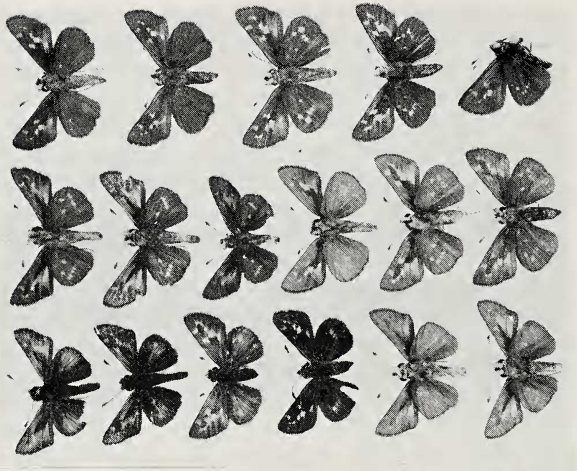
Quebec: Montreal, Terrebonne, Aylmer, Lakefield, Norway Bay, Shawbridge, Lanoraie, St. Anne de Bellevue, Rawdon, St. Maurice, Rigaud, Papineau Co., Gatineau Co., Pontiac Co.

New Brunswick: southern part.

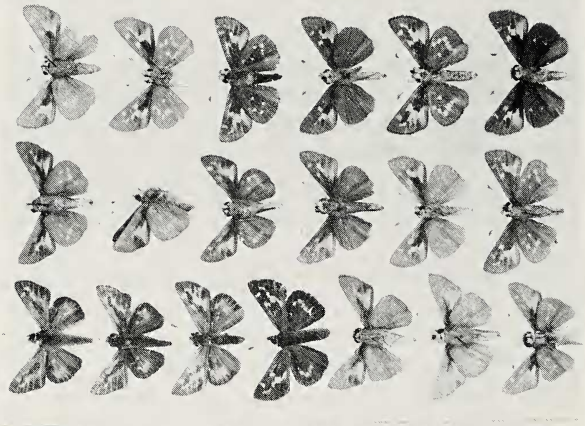
Ontario: Perth Rd., Frontenac Co.; Bruce Co.; Clarendon; Chaffey's Locks, Leeds Co.; Kent Bridge, Kent Co.; Kahshee Lake, Muskoka Distr.; Asperitos Id., Parry Sound Distr.; Gravenhorst, Muskoka Distr.; Georgian Bay; Ottawa; London; Dublin; Toronto; Simcoe; Bruce Co.;Algonquin Park, Parry Sound Distr.

Maine: Penobscot, Cumberland, Lincoln, York, Hancock, Washington, Somerset, Franklin.

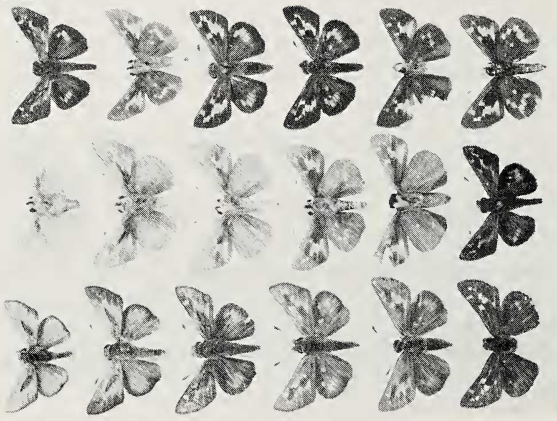
New Hampshire: Coos; White Mts.; Mast Yard.



Figs. 45-61



Figs. 26-44



Figs. 8-25

Figs. 8-25. *H. leonardus pawnee* (Figs. 8-18) and *H. l. leonardus* (Figs. 19-25). Ssp. *pawnee*: left column (top to bottom): m ups (upperside) Green Mtn., Jefferson Co., CO, 25 Aug. 1971, J. Scott; m ups same data; m ups Green Mtn., 4 Sept. 1969, J. Scott; f ups 3 mi. S. Sedalia, Douglas Co., CO, 3 Sept. 1967, R. Stanford; f ups Lakewood, CO, 3 Sept. 1960, J. Scott; f ups Little Missouri River, Billings Co., ND, 22 July 1970, J. Nordin; middle column: m und (underside) (ventral hindwing color no. 1) Green Mtn., 25 Aug. 1971, J. Scott; m und 3 mi. E. Wetmore, Custer Co., CO, 2 Sept. 1971, J. Scott; f und 3 mi. S. Sedalia, 3 Sept. 1967, R. Stanford; f und 1 mi. E. Parker, Douglas Co., CO, 11 Sept. 1968, R. Stanford; f und ½ mi. W. Bitter Lake, Day Co., SD, 25 Aug. 1971, J. Nordin; ssp. *leonardus*: m ups near N. Manchester, Kosciusko Co., IN, 27 Aug. 1970, E. M. Shull; right column: m ups Eggleston, VA, 26 Aug. 1964, G. Straley; m und Enfield, ME, 26 Aug. 1964, L. Grey; f ups near N. Manchester, 2 Sept. 1970, E. Shull; f ups Ida Center Rd., Monroe Co., MI, 28 Aug. 1971, L. Melton; f und near Woodbine, Cape May, NJ, 12 Sept. 1970, R. Stanford; f und Eggleston, 14 Sept. 1964, G. Straley.

Figs. 26-44. *H. leonardus leonardus* x *leonardus pawnee*, all from Sand Dunes State Forest, Sherburne Co., Minnesota. Left column: m ups 31 Aug. 1966, C. Hansen; m ups, 18 Aug. 1967, P. Nordin; f ups 29 Aug. 1971, J. Masters; f ups 19 Aug. 1967, P. Nordin; m und 19 Aug. 1967, P. Nordin; m und (ventral hindwing color rating no. 2), 19 Aug. 1967, P. Nordin; m und 31 Aug. 1966, C. Hansen; middle column: m und (color rating no. 4), 16 Aug. 1970, J. Nordin; m und (color rating no. 3), 29 Aug. 1971, J. Masters; m und 19 Aug. 1967, P. Nordin; m und 19 Aug. 1967, P. Nordin; f und 29 Aug. 1971, J. Masters; f und 25 Aug. 1969, J. Sorensen; right column: f und 25 Aug. 1969, J. Sorensen; f und 19 Aug. 1967, P. Nordin; f und 25 Aug. 1969, J. Sorensen; f und 25 Aug. 1969, J. Sorensen; f und 25 Aug. 1969, J. Sorensen; f und (color rating no. 6), 19 Aug. 1967, P. Nordin.

Figs. 45-61. *H. leonardus montana*, all J. Scott. Left column (top to bottom): m ups N. of Cheesman Lake, Jefferson Co., CO, 3 Sept. 1971; m ups Nighthawk, Douglas Co., CO, 28 Aug. 1969; f ups Nighthawk, 1 Sept. 1970; f ups Nighthawk, 1 Sept. 1970; m und Nighthawk, 12 Aug. 1971; m und Nighthawk, 29 Aug. 1971; middle column: m und Nighthawk, 12 Aug. 1971; m und Nighthawk, 28 Aug. 1969; m und Nighthawk, 1 Sept. 1970; f und (ventral hindwing color rating no. 2), Nighthawk, 28 Aug. 1969; f und Nighthawk, 29 Aug. 1971; f und Nighthawk, 28 Aug. 1969; right column: f und Nighthawk, 1 Sept. 1970; f und Nighthawk, 28 Aug. 1969; f und Nighthawk, 28 Aug. 1969; f und Nighthawk, 1 Sept. 1970; f und (color rating no. 5), N. of Cheesman Lake, 3 Sept. 1971.

Vermont: Windham.

Massachusetts: Barnstable, Nantucket, Essex, Middlesex, Bristol, Dukes, Worcester; Harwich Point; Pelham Hills; Hallowell (in Mass.?).

New Jersey: Camden, Ocean, Cape May, Middlesex, Burlington, Mercer,

Bergen, Union.

Rhode Island: Providence, Washington.

Connecticut: Hartford.

New York: Richmond, Nassau, Suffolk, St. Lawrence, Clinton, Jefferson, Essex, Lewis, Oswego, Hamilton, Warren, Washington, Fulton, Oneida, Albany, Schoharie, Columbia, Onondaga, Genesee, Erie, Livingston, Chautauqua, Cattaraugus, Allegany, Steuben, Yates, Cayuga, Seneca, Schuyler, Chemung, Tompkins, Tioga, Broome, Chenango, Delaware, Sullivan, Ulster, Orange, Dutchess, Rockland, Westchester, Greene.

Pennsylvania: Allegheny, Bucks, Butler, Chester, Clarion, Crawford, Delaware, Fayette, Montgomery, Montour, Lancaster, Somerset, Warren, Westmoreland, Bedford, Indiana, Schuylkill, Tioga, Susquehanna, Berks, Lackawanna, Monroe, Pike, Clinton, Potter, Centre.

Maryland: Montgomery, Garrett, Baltimore, Allegheny, Prince Georges, Charles, Ann Arundel.

District of Columbia: Washington.

Virginia: Arlington, Patrick, Madison, Giles, Montgomery, Prince William, Stafford, Powhatan.

West Virginia: Kanawha, Randolph, Nicholas, Upshur, Lewis.

North Carolina: Durham, Richmond, Buncombe, Avery, Guilford, Clay, Transylvania.

South Carolina: Greenville.

Georgia: Rabun.

Alabama: Cherokee, Tuscaloosa.

Louisiana: Madison Parish.

Tennessee: Morgan, Marion.

Kentucky: Larue, Jefferson, Meade.

Ohio: Franklin, Lorain, Athens, Lucas, Williams, Hocking, Jackson, Wayne, Ashland, Vinton.

Indiana: Perry, Brown, Lake, Randolph, Wabash, Kosciusko, LaGrange, Porter, Steuben, Pulaski.

Illinois: Vermilion, Mason, Cook, Peoria, McDonough, Jackson, Mason, Hancock, Schuyler.

Michigan: Monroe, Newaygo, Iosco, Allegan, Montcalm, Kalamazoo, Chippewa, Livingston, Houghton, Otsego, Oakland, Macomb, Grand Traverse, Presque Isle, Schoolcraft, Emmet, Cheboygan, Kalkaska, Crawford, Oscoda, Manistee, Roscommon, Ogemaw, Lake, Osceola, Mecosta, Huron, Ottawa, Kent, Clinton, St. Claire, Ingham, Jackson, Washtenaw, Wayne, Berrian, Brown, Van Buren, Dickinson.

Arkansas: Benton, Washington, Carroll, Ovachita.

Missouri: St. Louis, Iron, Camden, Barry, Greene, Franklin, Jefferson, St. Francois.

Kansas: Douglas.

Iowa: Scott, Des Moines, Polk, Audubon?, Winneshiek.

Wisconsin: Marinette, Eau Claire, Grant, Langlade, Milwaukee, Green, Sauk, Dane, Columbia.

Manitoba: Sandilands.

H. l. leonardus x *H. l. pawnee* (counties and localities)
121 males, 55 females examined

Wisconsin: Douglas (Dairyland, Jackson L. Boughner); Burnett (Crex Meadows near Grantsburg, J. L. Boughner).

Minnesota: Sherburne (Sand Dunes State Forest SSE Orrock and near Zimmerman, J. S. Nordin, P. D. Nordin, C. Hansen, J. Masters, J. T. Sorenson, W. Bergman); Anoka (Section 11, Coon Rapids Township, J. S. Nordin; Bunker Prairie, R. L. Huber); Wabasha (Kellogg, Allison Bolduc, Gary Korsmo; Kellogg Prairie, R. L. Huber); Goodhue (Eggleston, E. M. Brackney); Chisago (2 mi. N. Chisago City); Crow Wing (Brainard); Olmstead; Scott; Dakota.

H. leonardus pawnee (counties only for U. S.)
409 males, 139 females examined

Minnesota: Lac Qui Parle, Murray, Yellow Medicine, Chippewa, Pipestone, Clay, Lincoln, Norman, Swift.

Iowa: Poweshiek?, Woodbury.

Kansas: Smith.

Nebraska: Stanton, Boone, Dodge, Nemaha, Douglas.

South Dakota: Day, Meade, Harding, Pennington, Custer, Lawrence, Brookings, Marshall, Roberts.

North Dakota: Ransom, Bottineau, Williams, McKenzie, Morton, Grand Forks, Billings, Ramsey, Slope.

Manitoba: Aweme, Cartwright, Spruce Woods Forest Reserve near Hwy. 258.

Saskatchewan: Redvers.

Montana: Dawson, Custer, Big Horn, Prairie, Chouteau.

Wyoming: Platte, Sheridan, Laramie.

Colorado: Logan, Larimer, Weld, Boulder, Denver, Arapahoe, Jefferson, Douglas, El Paso, Custer, Pueblo, Morgan.

H. leonardus montana (counties and localities)
208 males, 239 females examined

Colorado: Douglas Co.: Sugar Creek 5 mi. NE Deckers (R. E. Stanford), Nighthawk 10 mi. NE Deckers, 4.3 mi. SE Deckers, 10 mi. SSE Deckers (all three J. A. Scott); Teller Co.: junction of Teller, Douglas, Jefferson, and Park Counties (R. E. Stanford); Jefferson Co.: 1 mi. N Cheesman Reservoir near Wigwam Creek (J. A. Scott), 6.9 rd. mi. up North Fork of South Platte River from town of South Platte (J. A. Scott), South Platte Hotel (R. E. Stanford & J. A. Scott), Deckers (R. E. Stanford).

Summary

Hesperia leonardus Harris, 1862

a. *leonardus leonardus* Harris, 1862
   ? *liberia* Plotz, 1883 (nomen dubium, dos Passos, 1960)
   ? *lidia* Plotz, 1883 (nomen dubium, dos Passos, 1964)
   stallingsi Freeman, 1943 (subjective synonym)
b. *leonardus leonardus* x *leonardus pawnee* (intergrade populations)
c. *leonardus pawnee* Dodge, 1874 (new combination)
d. *leonardus montana* (Skinner) 1911 (new combination)
   Type locality correction and restriction: town of Buffalo Creek,

Jefferson County, Colorado.
Lectotype designated Carnegie Museum.

Acknowledgments. Many people helped us in this project. We especially thank Charles A. Triplehorn (Ohio State University Museum), Julian P. Donahue (Los Angeles Natural History Museum), Charles Remington (Peabody Museum, Yale University), Howard V. Weems, Jr. (Florida Department of Agriculture, Gainesville), Frederick H. Rindge (American Museum of Natural History), Wilbur R. Enns (University of Missouri, Entomology Museum), Richard Heitzman, John T. Sorensen, John Masters, Roderick R. Irwin (Illinois Natural History Survey), Lutz J. Bayer (University of Wisconsin), John Hafernik, John S. Nordin, Philip D. Nordin, Clark Hansen, and C. Don MacNeill for information and loan of specimens. We also thank Arthur M. Shapiro, Steven J. Kohler, Charles V. Covell, Jr., Tim L. McCabe, Richard E. Gray, J. Bolling Sullivan, Frances McAlister, F. M. Brown, Bryant Mather, Roger M. Kuehn, Arthur C. Sheppard (Lyman Museum, McGill University), C. S. Quelch, Warren J. Kiel, Jack L. Harry, William Bergman, Robert Price, Mogens C. Nielsen, Walfried J. Reinthal, Clifford D. Ferris, Mike Fisher, Harry K. Clench (Carnegie Museum), William H. Howe, George Lewis (Canadian National collection), Gerald B. Straley, Lee J. Melton III, Lucien Harris, Jr., Richard B. Dominick, Ronald L. Huber, Jackson L. Boughner, F. Martin Brown, Ronald R. Gatrelle, William E. Sieker, H. Townes, Jr., Kurt Johnson, William McGuire, and Ernest M. Shull for helpful information.

Literature Cited

CLARK, A. H. & C. F. CLARK, 1951. The butterflies of Virginia. Smithsonian Inst., Washington, D. C. 239 p.

DETHIER, V. G., 1939. Early Stages of some Hesperiinae. Canad. Ent. 71: 117-118.

_____, 1948. Life history of *Hesperia leonardus*. Bull. S. Calif. Acad. Sci. 47: 1-2.

dos PASSOS, C. F., 1960. Taxonomic notes on some nearctic Rhopalocera. 1. Hesperioidea. 14: 24-36.

_____, 1964. A synonymic list of the nearctic Rhopalocera. Mem. Lepidopterists' Society No. 1.

EVANS, W. H., 1955. A catalogue of the American Hesperiidae in the British Museum. Vol. 4, Hesperiinae. London: British Museum of Natural History.

FERRIS, C. D., 1971. An annotated checklist of the Rhopalocera (butterflies) of Wyoming. Agric. Exp. Sta. Univ. Wyoming, Laramie, Science Monograph No. 23, p. 1-75.

FERRIS, C. D. & M. S. FISHER, 1977. *Charidryas flavula* B. & McD.: a question of identity. J. Res. Lepid. 16: 133-140.

FREEMAN, H. A., 1943. A new form of *Hesperia leonardus* (Harris) from the middle western United States (Lepid., Hesperiidae). Bull. Brooklyn Ent. Soc. 38: 153-154.

LAURENT, P., 1908. Notes on some early stages of some *Pamphila*. Ent. News 19: 408-417.

LEUSSLER, R. A., 1923. Notes on variation in 53 specimens *Pamphila pawnee* collected at Pilger, Nebraska, Sept. 2, 1922. Ent. News 34: 28.

MacNEILL, C. D., 1964. The skippers of the genus *Hesperia* in western North America

with special reference to California. Univ. Calif. Publ. Entom. 35: 230 p.

_____, 1975. Hesperiidae, In W. Howe (ed.) The butterflies of North America. Doubleday & Co., New York.

SCOTT, J. A., 1975a. Clinical intergradation of *Hesperia comma colorado* (Hesperiidae). J. Lepid. Soc. 29: 156-161.

_____, 1975b. Early stages of seven Colorado *Hesperia* (Hesperiidae). J. Lepid. Soc. 24: 163-167.

SCOTT, J. A. & G. R. SCOTT, 1978. Ecology & distribution of the butterflies of southern central Colorado. J. Res. Lepid. 17: 73-128.

SCUDDER, S. H., 1889. Butterflies of the eastern United States and Canada with special reference to New England. 3 vol. Cambridge, Mass. 1958 p.

_____, 1893. Brief guide to the commoner butterflies of the northern United States and Canada. Henry Holt & Co., New York. 206 p.

SHAPIRO, A. M., 1966. Butterflies of the Delaware Valley. Amer. Ent. Soc. Special Publ. 79 p.

SKINNER, H., 1911. New species or subspecies of North American butterflies. Ent. News 22: 412-413.

TIETZ, H. M., 1972. An index to the described life histories, early stages, and hosts of the macrolepidoptera of the continental United States and Canada. Allyn Museum of Entomology, Sarasota, Florida. 1041 p.